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Influence of differing land management on the invasion of North American tallgrass prairie soils by European earthworms

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Summary. European earthworms have come to dominate earthworm assemblages in most North American soils. The establishment of these invasive taxa is typically preceded by agricultural or other perturbation of the natural soil system. Grassland soils in the Flint Hills region of North America have escaped these perturbations because of their steep topography and stony soils; and as a consequence, still support native earthworms. Nevertheless, European taxa are invading these soils, and the conditions under which these invasions occur are unknown.

In fall of 1994 and spring of 1997 we sampled earthworms from experimental plots at Konza Prairie Research Natural Area in eastern Kansas, to assess the impacts of different land management practices on composition of the earthworm fauna in grassland soils. Since 1986, these plots have been subjected to all possible combinations of the following treatments: annually burned or unburned, annually mowed or unmowed, and annually fertilized (N and P) or unfertilized, totaling in eight treatments.

European taxa were significantly more abundant in unburned plots in samples collected in both 1994 and 1997 ($p = 0.03$ and $p = 0.07$ respectively). Furthermore, analysis of the 1997 data indicated a greater proportion of the earthworm community was composed of native taxa in plots which were mowed ($p = 0.08$), and in plots which were not fertilized ($p = 0.09$). The accumulation of litter on the soil surface associated with absence of fire and/or grazing may be partly responsible for changes observed in the earthworm community.

Our results suggest that land management practices may influence the suitability of these soils for European earthworms, and potential mechanisms for the differences observed in this study will be discussed.

Key words: Earthworms, *Diplocardia*, *Aporrectodea*, invasive species, fire

Introduction

Understanding the ecology of invasive exotic organisms is crucial to understanding their potential impacts on ecosystems, both in terms of interactions with native organisms, and changes in ecosystem structure and function (e.g. Scheu & Parkinson 1994; Burtelow et al. 1998). Many North American soils are currently inhabited by an entirely European (and/or Asian) earthworm fauna (Reynolds et al. 1970; Reynolds 1994), and others are currently being invaded by these exotic species.

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Early studies concerning the distribution and establishment of European earthworms (principally Lumbricidae) in North America suggested that these species were superior to native earthworms in their ability to compete for resources, and that native species were actively displaced by exotics in these competitive interactions (Smith 1928). However, more recent studies indicate that displacement of native earthworms is more likely the result of soil disturbances associated with human activities such as agriculture, logging, or land development (Stebbings 1969; Kalisz & Dotson 1989). Thus, the predominance of European earthworms in these soils is thought to be a function of their ability to tolerate soil disturbances, and not the direct result of competitive interactions with the native earthworm fauna.

Areas of North America once covered by tallgrass prairie have been subject to extensive soil disturbance, resulting from agricultural practices, and less than 5 % of this area remains as native prairie (Samson & Knopf 1984). Much of the remaining tallgrass prairie exists in small fragmented patches which lack many of the factors historically important for the structure and function of these grasslands (e.g. fire and grazing). However, the shallow, stony soils in the Flint Hills region of North America have escaped extensive disturbance associated with agriculture or urban development, and large tracts of native tallgrass prairie remain there. As a consequence, these soils are still inhabited by native North American earthworm taxa, including *Diplocardia* spp. and *Bimastos* spp. (James 1992). However, these ecosystems are not entirely undisturbed, nor are they immune to invasion by European earthworm species. Tallgrass prairie is dependant on some periodic disturbances such as fire or grazing (Knapp et al. 1998), and the suppression of these natural disturbances may influence the establishment of European earthworms.

Our objectives were 1) to assess the distribution of native and exotic earthworms relative to several land management practices, and 2) to determine the possible mechanisms driving the distribution patterns of native and exotic earthworms in these grasslands.

Materials and Methods

Earthworms were sampled from the Belowground Experimental Plots at the Konza Prairie Research Natural Area (KPRNA) a tallgrass prairie research site near Manhattan, Kansas, USA. The vegetation of KPRNA is characteristic of native tallgrass prairie and is dominated by the warm season tallgrasses *Andropogon gerardii, Sorghastrum nutans*, and *Panicum virgatum*, which co-occur along with many forb and shrub species (Gibson et al. 1993). The Belowground Experimental Plots were established in 1986 as part of the Long-Term Ecological Research program at KPRNA. A series of 64 12 m × 12 m plots were established on an Irwin silty clay loam (fine, mixed mesic, Pachic argiustoll) in a split strip-plot experimental design aimed at testing the effects of fire (annually burned vs. unburned), aboveground biomass removal (mowed vs. unmowed), and differing nutrient inputs (N fertilization, P fertilization, N and P fertilization, and no fertilization) on belowground processes and organisms (see Todd 1996, for details of the experimental design). Only plots receiving both nutrients (10.0 g N m^{-2} and 1.0 g P m^{-2}) and plots receiving no nutrient additions were used in this study.

Earthworms were sampled in October 1994 as part of the ongoing data collection in the Belowground Experimental Plots (a 20 cm × 50 cm × 20 cm deep soil monolith from each plot was passed through a 4 mm sieve in the field, and earthworms were collected and preserved in 70 % ethanol). A second set of samples was collected in April 1997 to assess treatment effects on earthworm community structure during the spring when earthworms are more abundant (James 1992) (a 25 cm × 25 cm × 25 cm deep soil monolith). Soils were stored at 4 °C until sorted by hand in the laboratory. Earthworms in these soils were killed in 70 % ethanol, and preserved in 5 % formalin. Earthworms were identified to genus (James 1990; Schwert 1990), and abundance data, as well as proportion of total community composed of native taxa, were analyzed using an ANOVA designed for the analysis of split strip-plot experiments (Todd 1996).

In order to assess potential relationships between earthworm community changes and vegetational changes associated with different management practices, plant data from KPRNA data archives for the Belowground Experimental Plots were used. These data included 1) grass biomass, 2) forb biomass, 3) previous years' surface litter, 4) current year's surface litter, and 5) total surface litter collected from two replicate 0.1 m^2 quadrats in each plot. Four year averages (1993-1996) for each of these vegetation parameters were regressed against the proportion of total earthworm community composed of exotic taxa. All data were log transformed to satisfy normality assumptions.

Results

Results of the 1994 sampling showed that the abundance (no. per m^2) of *Diplocardia* spp. was not significantly affected by any land management treatment (Fig. 1a). However, the abundance of *Aporrectodea* spp. in 1994 was significantly ($p = 0.03$) higher in unburned plots than in burned plots (Fig. 1a).

In 1994, there was a significant interaction ($p = 0.07$) between burning and fertilizer treatments on the proportion of the total earthworm community consisting of *Diplocardia* spp. Inspection of the data revealed that in treatment combinations where fertilization seems to have had an effect, that effect was to decrease the proportion of *Diplocardia* spp. (Fig. 2).

Results of the 1997 sampling showed trends among treatments which were similar to those of the 1994 sampling (Fig. 1b), including a greater abundance of *Aporrectodea* spp. in unburned plots ($p = 0.07$).

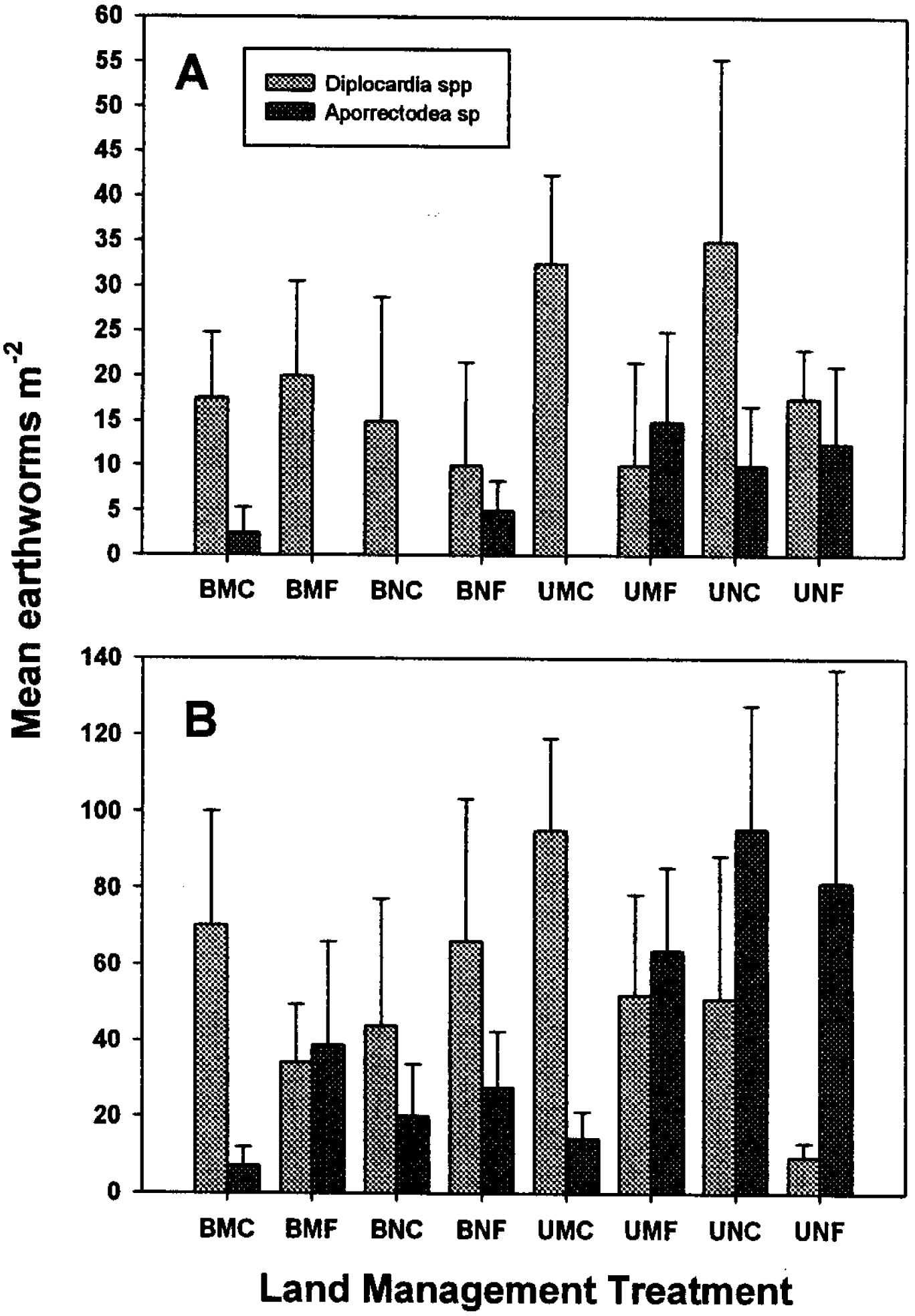

Fig. 1. Abundances of native and exotic earthworms relative to land management treatments in A) October 1994 and B) April 1997. Note differences between Y-axes
Note: B = burned annually, U = unburned, M = mowed annually, N = not mowed, C = unfertilized, F = nitrogen and phosphorus fertilizer added annually

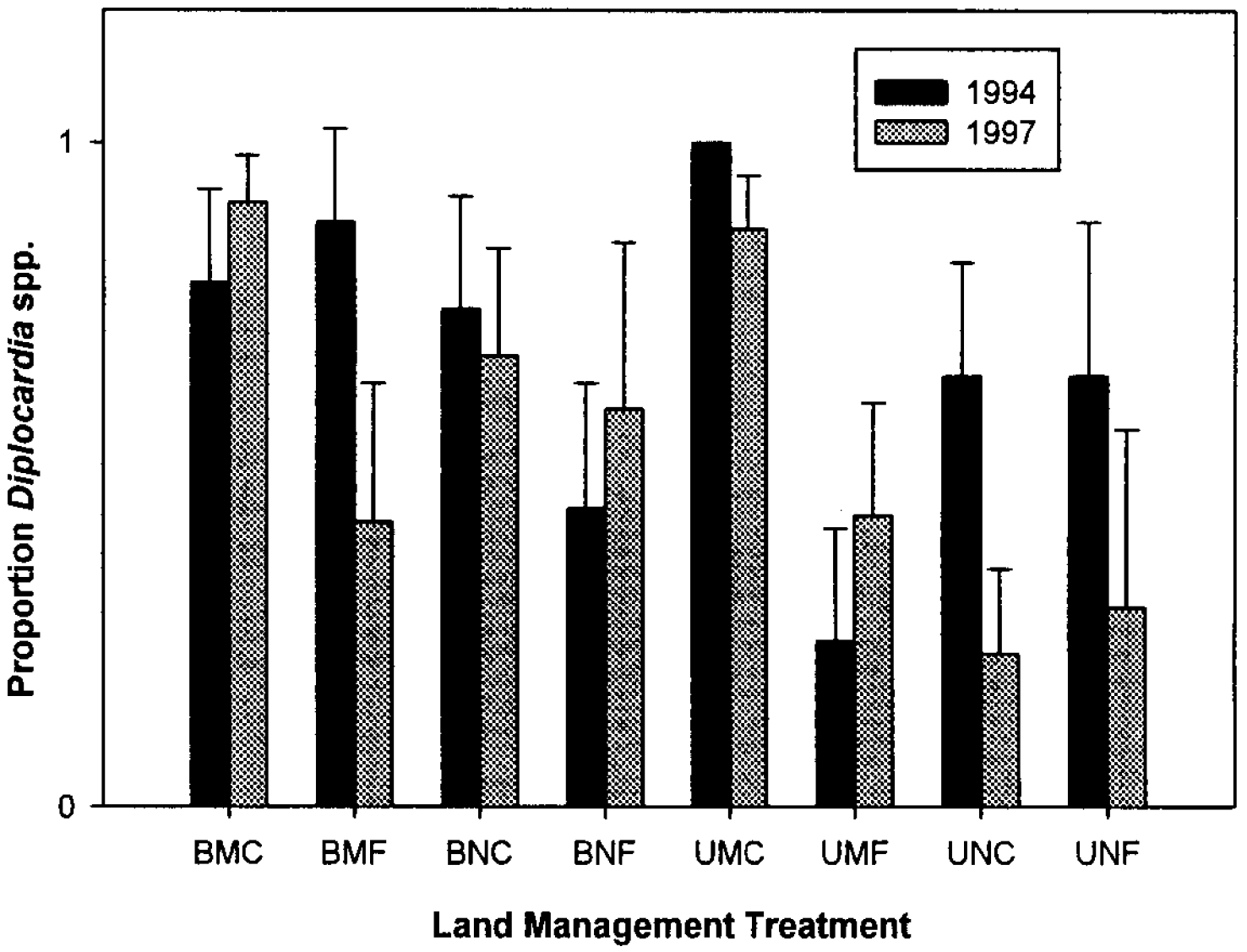

Fig. 2. Proportion of earthworm community composed of *Diplocardia* spp. relative to land management treatments (Note: X-axis labels as in Figure 2)

In contrast to the 1994 sampling, the proportion of the earthworm community that consisted of *Diplocardia* spp. in 1997 was significantly influenced by mowing ($p = 0.08$) as well as fertilizer ($p = 0.09$), but with no significant interaction between burning and fertilization. The effect of mowing was to increase the mean proportion of *Diplocardia* spp. in the earthworm community from 0.45 in unmowed plots to 0.66 in mowed plots (Fig. 2), while the effect of fertilizer was to decrease the mean proportion of *Diplocardia* spp. from 0.67 in control plots to 0.44 in the fertilized plots (Fig. 2).

Regression analysis of relationships between proportion of earthworm community consisting of *Aporrectodea* spp. and vegetation parameters revealed that only total surface litter mass was significantly related to earthworm community composition. The four year average (1993–1996) of total litter mass in experimental plots was significantly positively related to the proportional abundance of *Aporrectodea* spp. in 1994 as well as in 1997 ($p = 0.07$ and $p = 0.02$, respectively) (Fig. 3).

Discussion

The results of this study suggest that the distribution and abundance of invasive European earthworms in North American tallgrass prairie soils can be attributed, in part, to land management practices. Furthermore, in areas where exotic earthworms are most prevalent, it appears that displacement of native species may be occurring. Particularly notable are the differences in earthworm community structure between what we consider to be the two extreme land management treatments -annually burned, mowed, without fertilizer, and unburned, unmowed, with supplemental nutrients (BMC vs. UNF on Fig. 1). In 1997, the earthworm communities were most dissimilar in these two extreme treatments, with native earthworm species dominant in the BMC plots and exotic earthworms most dominant in UNF plots (Fig. 1). The plots with the most intense "natural" disturbance regime (burned, mowed, with no added nutrients) most closely approximate conditions prevalent prior to European settlement (frequently burned and grazed). These plots also most closely represent floristic and edaphic conditions of tallgrass prairie (Collins et al. 1998; Knapp & Seastedt 1986), and our study

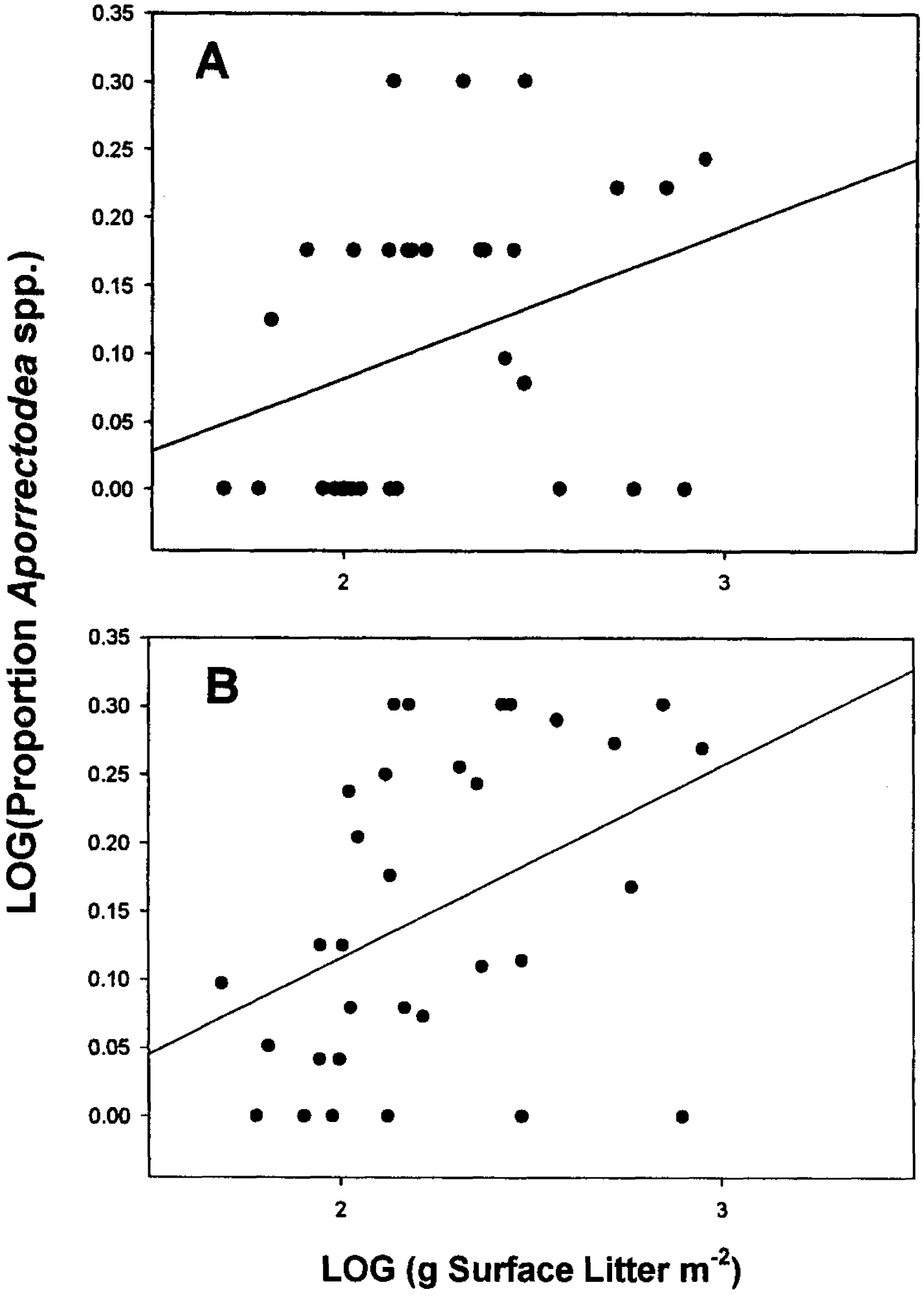

Fig. 3. Relationship between surface litter accumulation, and proportion of *Aporrectodea* spp. occurring in belowground plots during A) 1994 sampling andB) 1997sampling

demonstrates that this is true of the earthworm community in these plots as well. Previous studies of earthworm distributions in tallgrass prairie with respect to fire treatments have shown the abundance of *Diplocardia* spp. to be greater in annually burned prairie relative to prairie from which fire had been excluded for eight years (James 1982). Results of the current study differ somewhat from James (1982), as we found no effect of burning on the absolute abundance of *Diplocardia* spp., although the relative abundance of *Diplocardia* spp. was favored by burning (Fig. 2). One potential explanation for the discrepancy between the two studies is the virtual absence of exotic taxa in the soils sampled by James (he reports only a single individual of *Aporrectodea* spp.), and therefore the absence of any effects on distributions arising from interactions between the two taxa.

One effect of suppressing fire and grazing disturbances in tallgrass prairie is the accumulation of plant litter on the soil surface, and the land management treatments utilized in the belowground plot experiment at KPRNA result in continuum of surface litter accumulation. Indirect effects of this litter accumulation include increased soil moisture and decreased soil

temperature, particularly in the early growing season. We suggest that microclimatic consequences of differing land management practices may contribute to changes in earthworm communities in tallgrass prairie.

Fire also influences the amount and quality of plant inputs belowground, which could affect the distribution of earthworms. Both the biomass and C:N ratio of live roots is greater in annually burned plots compared to burned plots (Blair 1997; Ojima et al. 1994). The lower quality plant tissue could be a factor limiting the expansion of exotic earthworms in tallgrass prairie. However, to date, no experiments have separated the effects of changes in soil climate, belowground plant production, and belowground resource quality associated with fire or mowing with regard to responses of the earthworm community in tallgrass prairie.

In spite of the correlative nature of this study, and the difficulty in identifying the specific mechanisms underlying invasion by exotic earthworms, our study demonstrates that relatively short term departures from natural disturbance regimes can result in detectable changes in the abundances of native and exotic earthworm taxa in these soils. An understanding of the relationship between land management and the distribution of native and exotic earthworms may help to predict changes in biogeochemistry of soils as changes in land cover and land use continue in the Flint Hills region.

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